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Simulation of the Effect of Increased Atmospheric CO₂ on Assimilation and Transpiration of a Closed Crop Canopy¹

J. Goudriaan, H. H. van Laar, H. van Keulen and W. Louwse

Introduction

All terrestrial vegetation is exposed to a steadily growing background concentration of CO₂ (ca. 1.5 ppmv y⁻¹ at 340 ppmv background) due to release of CO₂ by combustion of fossil fuel. The rate of increase of atmospheric CO₂ corresponds to only about 60% of the CO₂ production from fossil fuel. Most of the remaining 40% is absorbed by the ocean. There is continuous exchange of carbon between the biosphere and the atmosphere. At present there is probably a net absorption by the biosphere of about 7% of the CO₂ from fossil fuel [9, 1].

It is a classic observation that aerial CO₂ is necessary for plant growth and that CO₂ enrichment usually has a stimulating effect on growth rate [19, 21]. To allow CO₂ diffusion into the leaves stomata must be open, which at the same time exposes the wet cell surfaces to the drying effect of the ambient air. An increase in atmospheric CO₂ facilitates the plant's dilemma to adjust stomatal aperture in such a way that transpiration is kept within acceptable limits, but that at the same time assimilation is not choked too much.

To examine the effect of an increase in atmospheric CO₂ concentration the simulation model BACROS [20] is applied as by van Keulen et al. [10], but with the following improvements:

- An aerodynamic resistance, calculated on the basis of the logarithmic wind profile, is inserted above the crop canopy. This resistance modifies the microclimate and moderates high fluxes.
- The effect of CO₂ on the CO₂-assimilation light response curve of individual leaves has been reformulated, especially in view of interactions with photorespiration.

Stomatal regulation

Van Keulen et al. [10] present literature data [18, 11, 8, 13] indicating the existence of three types of stomatal behaviour:

- A strong feedback of CO₂ on stomatal aperture, so that the internal CO₂ concentration (i. e. the concentration inside the stomatal cavity) is stabilized at a characteristic value. In this situation an increase in atmospheric CO₂ concentration will not

alter assimilation because the photosynthetic apparatus is not exposed to a different CO₂ environment. However, stomata will partially close, consequently transpiration will be strongly reduced, which in case of water-limited production will lengthen the growing season.

- A weak feedback of CO₂ on stomatal aperture, resulting in an internal CO₂ concentration that is proportional to the external concentration. This type of behaviour is probably the most frequent one [17]. In this case the benefit of an increased external CO₂ concentration is shared between higher assimilation and lower transpiration. Stomatal aperture is reduced and hence transpiration, but not enough to suppress the effects on assimilation. Also in this situation a longer growing season may be the result.

- No feedback of CO₂ concentration on stomatal aperture. It seems that such behaviour requires absence of waterstress throughout, or is operative under very high temperatures. In this situation, transpiration will not be affected by external CO₂ concentration, but assimilation will be stimulated.

Whatever the type of stomatal behaviour, the transpiration-assimilation ratio will be reduced by increased CO₂.

Modelling the aerodynamic or turbulence resistance

Its value

The value of the turbulence resistance is calculated applying the classical theory of the logarithmic wind profile [14]:

$$r_t = 0.74 \ln^2 \left(\frac{z_r - d}{z_0} \right) / (k^2 u_r) \quad (1)$$

The reference height, z_r , is assumed to be one meter above crop height z_c (about 1.25 m). With a zero plane displacement, d , of about $0.7 z_c$, a roughness length, z_0 , about $0.1 z_c$. Von Karman's constant, k , about 0.4, and windspeed, u_r , about 2 m s^{-1} , the resistance is of the order of 10 to 20 s m^{-1} . Stomatal resistances are of the order of 100 to 200 s m^{-1} , but because the various leaf layers act in parallel, the resulting crop resistance is much lower and is of the order of 50 s m^{-1} . Therefore, the aerodynamic resistance in series with stomatal resistance can easily reduce transpiration by 30%.

¹The manuscript was improved by Dr. Peisker's valuable comment.

Its effect on assimilation

Under high levels of irradiance the rate of net CO₂ assimilation of a crop may reach values of 60 kg CO₂ ha⁻¹ h⁻¹, causing a drop of 10 to 20 ppmv across the turbulence resistance, *r_t* (Fig. 1). This drop in itself may affect the assimilation rate, so that an iterative procedure seems required. To avoid that procedure, the CO₂ content of the air at crop level is defined as a state variable, with a time constant artificially fixed at 1 hour. In this way the iteration is avoided at the expense of a delay of 1 hour in the CO₂ drop. Even under high irradiance the drop does not exceed 20 ppmv, so that the feedback effect on assimilation is limited. Moreover, these deviations have opposite effects in the morning and in the afternoon so that they practically cancel out as far as daily totals are concerned.

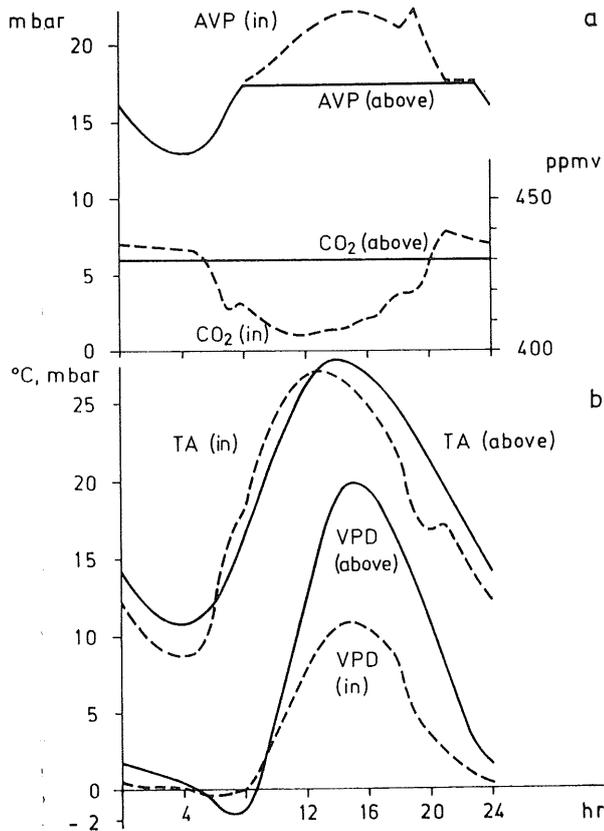


Fig. 1. Diurnal courses of some air properties, simulated for a C₄ species, non-regulating stomata, clear sky, 430 ppmv CO₂, 50° N. L. a) Water vapour pressure (AVP) and CO₂ above and inside the canopy b) Air temperature (TA) and vapour pressure deficit (VPD) above and inside the canopy

Its effect on transpiration

At a given stomatal resistance the response of transpiration rate to the vapour pressure deficit in the air is linear. This linearity can be used to solve directly the energy balance equations, including the effect of the turbulence resistance. For this purpose, it is assumed that all leaves inside the crop canopy are exposed to an identical ambient temperature and humidity, derived from the atmospheric values modified by the turbulence resistance:

$$T_{in} = T_a + \frac{r_t}{\rho c_p} \sum LA_i W_i \quad (2a)$$

$$e_{in} = e_a + \frac{\gamma r_t}{\rho c_p} \sum LA_i \lambda E_i \quad (2b)$$

with,

<i>T_a</i>	air temperature above the crop	°C
<i>T_{in}</i>	air temperature within the crop	°C
<i>e_a</i>	air humidity above the crop	mbar
<i>e_{in}</i>	air humidity within the crop	mbar
<i>W_i</i>	sensible heat flux per unit leaf area	W m ⁻²
<i>λE_i</i>	latent heat flux per unit leaf area	W m ⁻²
<i>LA_i</i>	leaf area index of layer <i>i</i>	-
<i>γ</i>	psychrometric constant (0.67)	mbar °C ⁻¹
<i>ρc_p</i>	volumetric heat capacity of the air	J m ⁻³ °C ⁻¹ (1200).

The summations in Eqns. 2a and 2b are performed over all leaf layers and yield the fluxes per unit surface area. The vapour pressure deficit inside the crop canopy, *VPD_{in}*, is now obtained from:

$$VPD_{in} = VPD_a + s(T_{in} - T_a) - (e_{in} - e_a) \quad (3)$$

where *s* is the slope of the saturated vapour pressure curve at air temperature. This linearized equation closely approximates the true curved relation. Substituting Eqns. 2a and 2b yields:

$$VPD_{in} = VPD_a + \frac{r_t}{\rho c_p} \sum LA_i (sW_i - \gamma \lambda E_i). \quad (4)$$

Eqn. 4 shows that vapour pressure deficit, and hence crop transpiration rate may either increase or decrease as a result of the presence of the turbulence resistance. The direction of change is determined by the ratio of sensible and latent heat flux (Bowen ratio). With fully open stomata and high transpiration rate the vapour pressure deficit inside the crop is lower than that above it, but with almost closed stomata and low transpiration the reverse is true. Therefore stomatal effects on transpiration tend to be reduced.

The final effect depends on the magnitude of the fluxes in Eqn. 4 which are a function of *VPD_{in}* itself. The sensible and latent heat fluxes per unit leaf area are defined as:

$$W_i = \frac{\gamma^* R_n - \delta}{s + \gamma^*} \quad (5a)$$

$$\lambda E_i = \frac{s R_n + \delta}{s + \gamma^*} \quad (5b)$$

where

$$\gamma^* = \gamma \frac{r_b + r_l}{r_b} \quad (6)$$

and

$$\delta = \frac{VPD_{in} \rho c_p}{r_b} \quad (7)$$

with

*γ** apparent psychrometric constant mbar °C⁻¹

R_n total absorbed radiation per leaf area W m⁻²

δ drying power of the air mbar W m⁻² °C⁻¹

r_b leaf boundary layer resistance s m⁻¹

r_l leaf resistance (stomata/cuticula) s m⁻¹.

Substituting Eqns. 5, 6 and 7 into Eqn. 4 and solving for *VPD_{in}* yields:

$$VPD_{in} \left\{ 1 + r_t (s + \gamma) \sum \frac{LA_i}{r_b (s + \gamma^*)} \right\} = VPD_a + \frac{s r_t}{\rho c_p} \sum \frac{R_n r_l \gamma}{r_b (s + \gamma^*)} LA_i. \quad (8)$$

This equation enables a direct calculation of the vapour pressure deficit inside the crop canopy. Typical time courses of the VPD above and inside the crop are shown in Fig. 1b.

Time and spatial resolution

In the calculations time steps of one hour were used. In Eqn. 8a summation for all leaf classes is required twice, before the vapour pressure deficit can be calculated. Once the vapour deficit inside the crop canopy is known, the transpiration flux can be found by another summation over the same leaf classes. If time steps of one day are used, these two summations must be consequently done each time step. For our purpose the summations were executed simultaneously, thereby accepting the fact that correction terms in Eqn. 8 are one hour delayed. When smooth diurnal courses of weather are used, as in this example, the effect of this error is negligible.

We considered the canopy space as a well mixed reservoir, connected with the atmosphere through a single aerodynamic (or turbulence) resistance. This simplification is permissible if one is not interested in the profiles inside the canopy themselves [7].

Modelling the effect of CO₂ on the CO₂ assimilation—light response curve

The light response curve of leaves is described by an asymptotic exponential (monomolecular) equation. This equation often gives a better fit to experimental data than the rectangular hyperbola [15, 3]. Three parameters characterize the response curve: the light saturated assimilation rate F_m , the initial slope ϵ and the dark respiration rate R_d :

$$F_n = (F_m + R_d) (1 - \exp(-\epsilon H / (F_m + R_d))) - R_d \quad (9)$$

with,

$$F_n \text{ actual assimilation rate} \quad \text{kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1}$$

$$H \text{ absorbed radiant flux in the} \quad \text{J m}^{-2} \text{ s}^{-1}$$

400 to 700 nm range.

CO₂ concentration presumably does not affect the dark respiration, but it may influence both maximum assimilation rate and initial slope. It is assumed that the inherent assimilatory capacity of the photosynthetic apparatus by far exceeds the constraints imposed by light and CO₂. Therefore, under high irradiance the affinity of the carboxylating enzyme limits assimilation and the response to CO₂ is linear. We can then simply use:

$$F_m = (C_i - \Gamma) / r_x \quad (10)$$

where C_i is the CO₂ concentration inside the stomatal cavity, Γ is the CO₂ compensation point and r_x is the apparent mesophyll resistance. This equation has the same structure as that for a diffusion-limited uptake. However, the limiting step is not diffusion, but carboxylation. Therefore, the so-called mesophyll resistance can be largely identified with the carboxylation resistance. In BACROS this mesophyll resistance is standardized at 260 s m⁻¹ for C₃ plants and 110 s m⁻¹ for C₄ plants, and the CO₂ compensation point Γ at 50 ppmv and 5 ppmv respectively (Table 1). At typical values of 210 and 120 ppmv for the CO₂ concentrations in the stomatal cavity, these values correspond to about 40 and 70 kg CO₂ ha⁻¹ h⁻¹ respectively. When the stomatal resistance is not regulated, the internal CO₂ concentration and the maximum net assimilation rate may be higher.

For modelling purposes we assume that R_d in Eqn. 9 is independent of light intensity. Consequently we can also write Eqn. 10 as

$$F_m = F_g - R_f - R_d \quad (11)$$

with F_g the maximum gross assimilation, and R_f the photorespiration flux.

When F_g is equal to C_i / r_x (no constraint by a maximum enzyme activity) we obtain

$$R_f + R_d = \Gamma / r_x \quad (12)$$

In C₄ species R_f is zero and Γ is entirely determined by R_d (Table 1). In C₃ species the dark respiration rate is responsible for about 12 ppmv out of the 50 in total. The remaining 38 ppmv is caused by photorespiration and may be called the CO₂-photo-compensation point Γ^* [12].

Its value increases linearly with the oxygen concentration. The photorespiratory fraction R_f / F_g is equal to C_i / Γ^* [4] and independent of the level of irradiance. Still, photorespiration is relatively more detrimental at low light intensities than at high intensities. Not only is RuDP withdrawn from carboxylation, but also are the oxygenation products recovered by costly energy so that gross photosynthesis is reduced as well. Using data of Peisker and Apel [16] and of Farquhar and Von Caemmerer [5] the apparent initial light use efficiency is given by:

$$\epsilon = \epsilon_0 \frac{C - \Gamma^*}{C + 2\Gamma^*} \quad (13)$$

The gross efficiency ϵ_0 is higher in C₃ than in C₄ plants [2] but this advantage is more than offset at normal oxygen and CO₂ concentrations (Table 1).

The value of C to be used in Eqn. 13 is the ambient CO₂ concentration, since the initial efficiency refers to the photosynthetic activity close to the light compensation point where almost no gradient exists between leaf and air. At 300 ppm the multiplication factor in Eqn. 13 is about 0.68.

Table 1. Some characteristic values in leaf photosynthesis of C₃ and C₄ plants

	C ₃	C ₄
F_m	40	70 kg CO ₂ ha ⁻¹ h ⁻¹
C_i (regulated)	210	120 ppmv
Γ	50	5 ppmv
Γ^*	38	0 ppmv
r_x	260	110 s m ⁻¹
R_d	3	3 kg CO ₂ ha ⁻¹ h ⁻¹
ϵ_0	16.7	14 μg CO ₂ J ⁻¹ (PAR absorbed)
ϵ	11.5	14 μg CO ₂ J ⁻¹ (PAR absorbed)

In these units the product of resistance and flux must be divided by a conversion factor of 66 to find the CO₂ drop in ppmv.

Simulation conditions

As a standard day, the 21st of June is used, with a maximum and minimum air temperature of 27.8 and 10.8°C respectively, a water vapour pressure of 17.5 mbar in daytime and an average windspeed of 1.2 m s⁻¹. In daytime the windspeed is 1.6 m s⁻¹ and at night 0.8 m s⁻¹, with the transitions at 6 and 18 h resp. These air conditions are used as driving forces at a level of 1 m above the crop canopy (Fig. 1). As to radiation, a clear day and an entirely overcast day are simulated. The daily total global radiation at a clear day is 30 MJ m⁻² at 50° N. L., and one fifth of that under overcast conditions. The crop characteristics for the C₃ and C₄ type of plants are those of Table 1. The LAI is 4, the weight of crop is 5000 kg d. m. ha⁻¹, the end crop height is 1.25 m. The external CO₂ concentrations are assumed to be 330 and 430 ppmv, respectively.

Results

Diurnal courses (Fig. 1)

As an illustration of the dynamic behaviour of the model the situation with the highest fluxes (C₄ species, non-regulating stomata, clear sky, 50° N. L., 430 ppmv CO₂) is presented. In Fig. 1 both the vapour pressure above the crop canopy (AVP) and the simulated vapour pressure at an average level inside the

crop (AVP_{in}) are given. The vapour pressure difference may reach as much as 5 mbar. To support the high latent heat loss sensible heat loss is negative, and so the air temperature shows a drop of about 2 to 3°C.

As a consequence of the higher vapour pressure and lower air temperature in the canopy, the vapour pressure deficit is drastically reduced, and the transpiration flux with it. The peak at 19 h is caused by the sudden drop in wind speed, that occurred one hour before.

The diurnal course of the CO₂ concentration of the air inside the canopy is given in Fig. 1. The maximum drop of 25 ppmv at noon does not impose a serious restriction on the assimilation rate. These results show that the restriction of the turbulence resistance acts much stronger on transpiration than on assimilation.

Daily totals (Table 2, Fig. 2)

Compared to a previous simulation study [10] the daily total transpiration for the highest flux situation, as discussed above, dropped from 11 mm d⁻¹ to 7.5 mm d⁻¹ now. This is certainly an extreme case, but it does illustrate the importance of the turbulence resistance. Not always the transpiration rate is reduced. Under high irradiance and relatively closed stomata (C₄ species, fixed internal CO₂ concentration, clear sky, 50° N. L., 430 ppmv) the daily transpiration increased from 3.2 mm d⁻¹ in the previous study to 3.7 mm d⁻¹ here. Because of the rather high share of sensible heat loss in the energy budget, the turbulence resistance increased air temperature at crop level and the vapour pressure deficit decreased, notwithstanding a simultaneous increase in actual vapour pressure.

The results in Table 2 show that the transpiration/assimilation ratio is practically independent of radiation when stomatal regu-

Table 2. Simulated daily totals of net assimilation (A) in kg CO₂ ha⁻¹ d⁻¹ and of transpiration (T) in mm H₂O d⁻¹ for three types of stomatal regulation and two CO₂ concentrations of the atmosphere. The transpiration-assimilation ratio (T/A) is expressed in kg H₂O kg⁻¹ CO₂

	330 ppmv			430 ppmv		
	A	T	T/A	A	T	T/A
C₃ species						
fixed internal CO ₂						
clear sky	656	4.73	72.2	710	3.69	51.9
overcast sky	277	1.84	66.5	301	1.44	47.8
internal CO ₂ proportional to external						
clear sky	660	4.84	73.4	812	4.65	57.2
overcast sky	280	1.98	70.6	317	1.81	57.2
non-regulating stomata						
clear sky	667	6.48	97.1	820	6.44	78.5
overcast sky	287	3.88	135.2	324	3.87	119.5
C₄ species						
fixed internal CO ₂						
clear sky	979	4.55	46.5	982	3.69	37.6
overcast sky	356	1.55	43.6	359	1.29	36.0
internal CO ₂ proportional to external						
clear sky	1010	4.72	46.7	1130	4.36	38.6
overcast sky	360	1.61	44.8	372	1.43	38.5
non-regulating stomata						
clear sky	1108	7.48	67.5	1248	7.44	59.6
overcast sky	377	4.65	123.4	388	4.65	120.0

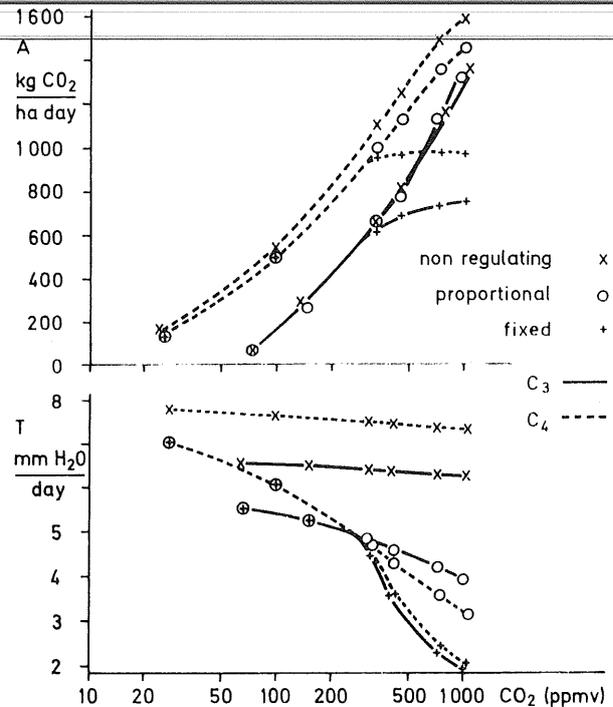


Fig. 2. Simulated daily net assimilation and water use efficiency of a C₃- and a C₄ species for a clear sky in June as a function of atmospheric CO₂. Three types of stomatal regulation are used (see text)

lation occurs. For both types of plants this ratio drops by about 20% when the CO₂ concentration of the air increases from 330 to 430 ppmv.

The turbulence resistance tends to dampen the extreme differences caused by the stomata themselves, and it reduces the range of their regulatory power. Even so, there is still a variation of a factor 2 to 3 in transpiration efficiency, dependent only on the stomatal regulation mechanism. According to these results the importance of stomatal regulation further increases with increasing atmospheric CO₂ concentration.

This is also demonstrated in Fig. 2, where simulated daily net assimilation and water use efficiency are plotted as a function of atmospheric CO₂, ranging from 25 to 1000 ppmv. The net assimilation is surprisingly well related to CO₂ on a logarithmic scale, at least when stomatal regulation occurs. Therefore daily assimilation can be well approximated by:

$$A = A_0 (1 + \beta \ln(C/C_0)) \quad (14)$$

where C₀ and A₀ stand for a reference CO₂ concentration and the corresponding assimilation. The coefficient β is called the biotic growth factor [6]. According to our simulation β is about 0.4 for C₄ and 0.8 for C₃ species with 330 ppmv as reference concentration. Although this logarithmic function has no physiological background and is not an a-priori model property, it is still a good representation of the overall model behaviour within the studied range of CO₂.

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Some Aspects of the Water Relations Between Different Organs of the Same Plant

Pierre Cruiziat

Introduction

The expansion of the studies on plant water relationships has been very important for the last thirty years. Three levels of investigation can be distinguished: isolated organs (leaf, root, stem...); plant as a whole; crop. Remarkable progress has been made on this third level with the development of concepts and methods of evapotranspiration. Concerning the first and the second levels the major attainments consist of: ● More clarity and standardization on definitions concerning the physical state of water in cells and tissues, with the general acceptance of the water potential concept as being the most appropriate quantity to characterize the state of water in the soil-plant-atmosphere continuum. ● Development of new techniques for measuring this water potential, especially micropsychrometer and pressure chamber (or Scholander bomb). ● Better knowledge of the water characteristics and properties of plant organs, specially owing to the use of the theory of the pressure-volume curves. ● Increasing interest in the physiology of water stress. Nevertheless beside these advances, an important chapter of the plant water relations has been missed: the water relations between organs of the same plant. This is yet an important aspect of the water physiology of a plant which is able to maintain a relative water homeostasis in a variable environment. For example, during a sunny day each leaf of the same plant could be exposed successively to sun and shade. Therefore, there is probably a continuous adjustment of the internal fluxes to satisfy at any

time the water demand of every part of the plant. This adjustment supposes variable fluxes between organs, depending on climatic conditions, availability of water in soil, state of organs, etc. The description and explanation of these internal fluxes and of their regulation may well constitute the most specific aspect to the water relationships of a plant as being a living organism. The aim of this paper is to give a brief assessment of what is known concerning water relations between organs of the same plant and to show some ways to improve our knowledge in this field of plant physiology.

I. What is known concerning the water relationships between organs of the same plant?

We will concern ourselves with two aspects: structural and functional.

1.1. Structural aspects

a) The vascular system of a plant is often of an extreme complexity. Most of the anatomical works only deal with a minor part of this system (there are some remarkable exceptions like [7, 3] because the classical methods are not adapted to give a complete picture of this complex network. Two authors [13, 14] developed only quite recently a new method, the so-called "optical shuttle method" or "the motion picture analysis" which permits description of the three dimensional structure of the vascular patterns in higher plants. It has been used to analyse the vascular system of

